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Impact of cyclones and aquatic macrophytes on recruitment and landings of tiger prawns *Penaeus esculentus* in Exmouth Gulf, Western Australia

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ABSTRACT

The cover of seagrasses and macroalgae, landings and fishery-independent measures of spawning stock and recruitment for brown tiger prawns, were monitored immediately following a major cyclone in Exmouth Gulf, Western Australia in March 1999. Anecdotal evidence on the extent of seagrass from 1990 to 1998 suggests that the cyclone caused a major, immediate disruption and loss of the seagrass/macroalgal beds (to $\leq$2% cover), the critical prawn nursery habitat, and mangroves in the shallow inshore waters of the system. Prawn landings and recruitment to the fishery were not affected in the year of the cyclone, but were markedly lower in the two years immediately afterwards and then increased as the cover of macrophytes increased to over 40% in 2003. Tiger prawn landings and catch rates were not affected in Shark Bay, a system 500 km south of Exmouth Gulf that did not experience cyclonic disturbance. Seagrasses in Exmouth Gulf showed a succession of species from small colonising species (*Halophila ovalis* and *Halodule uninervis*) to larger, broad-leaved species (*Cymodocea serrulata*, *Syringodium isoetifolium*) only two years after the cyclone. The recruitment and landings of tiger prawns were correlated significantly with the total cover of macroalgae and seagrass. The large loss of seagrass and macroalgae reduced the settling habitat for postlarvae and the nursery habitat for juvenile tiger prawns, probably leading to the lower recruitment to the fishery. These findings suggest that the extent of seagrass and macroalgae are some of the factors defining the productivity of the tiger prawn fishery in Exmouth Gulf.

1. Introduction

Coastal habitats, particularly vegetated habitats such as seagrass, mangroves and salt marsh are important habitats supporting fisheries production and biodiversity (e.g. Manson et al., 2005; Gillanders, 2006; Lotze et al., 2006; Waycroft et al., 2009). The area and linear extent of aquatic macrophytes, such as mangroves and salt marshes, have been correlated with total catch, catch per unit effort and/or maximum sustainable yield, particularly for penaeid prawns or shrimp (Staples et al., 1985; Browder et al., 1989; Loneragan et al., 2005; Manson et al., 2005). Vegetated habitats are hypothesised to provide an enhanced food supply, increased survival due to the provision of refuges from predation, and reduced wave action and water flow that stabilises sediments for fish and invertebrates (e.g. Bell and Pollard, 1989; Hatcher et al., 1989; Robertson and Blaber, 1992; Heck et al., 2003; Manson et al., 2005). Seagrasses and algae also provide important feeding habitats for species of conservation significance, such as dugongs and turtles (Gales et al., 2004). These coastal habitats are facing increasing threats from anthropogenic influences (e.g. Costanzo et al., 2001; Jackson et al., 2001; Gillanders, 2006) and since 1990, the loss rates of seagrass ecosystems have been similar to those for mangroves, coral reefs and tropical rainforests, making them among the most threatened ecosystems on earth (Waycroft et al., 2009).

The relationships between the structure of seagrass and the abundance of animals have been studied through correlation

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analysis (e.g. Orth and Heck, 1980; Bell and Westoby, 1986; Worthington et al., 1992; Loneragan et al., 1998) and, at smaller spatial scales, through experimental manipulation (e.g. Bell and Westoby, 1986; Connolly, 1994; Jenkins and Sutherland, 1997; Loneragan et al., 2001; Gillanders, 2006). As Worthington et al. (1992) noted, most of the correlation studies have documented patterns within individual beds and have not considered whether the recruitment of larvae and early juvenile stages affects the patterns of distribution and abundance across larger geographic areas. More recent research has shown that the proximity of mangroves to seagrass influences the value of seagrass as a nursery habitat for fish (Nagelkerken et al., 2001) and prawns (Skilleter et al., 2005). The magnitude of recruitment in the early life history stages and the 'carrying capacity' of the habitat are important factors for understanding the links between seagrass beds as juvenile habitat and the productivity of adjacent fisheries that the juveniles subsequently recruit to.

Gillanders (2006) reviewed the documented cases of seagrass loss that showed strong evidence of effects on fish and fisheries. Despite the large number of cases where major losses of seagrass and other submerged aquatic vegetation had been documented, few studies have demonstrated a link between declining seagrass and declining fish and fisheries production (see also Heck et al., 2003). One exception was in Westernport Bay in temperate south-eastern Australia, where over a 20-year period spanning the 1970s and the 1980s, a 70% decline in seagrasses was paralleled by a 40% decline in commercial fish catches (Jenkins et al., 1993; Hobday et al., 1999). Other factors such as overfishing, a reduction in fishing effort and a number of years of poor larval recruitment may also have contributed to the reported decline in catches in this system, confounding attempts to determine the relative importance of seagrass loss to the fisheries decline (Jenkins et al., 1993; Gillanders, 2006). Another case of seagrass loss leading to a decline in commercial fishery production has been reported in the Gulf of Carpentaria in tropical Australia, where a loss of about 183 km^2 of shallow, littoral seagrass was followed by a change in the composition of juvenile prawn assemblages in shallow water habitats and a 10% decline in tiger prawn catches in the adjacent, offshore waters of the fishery (Poiner et al., 1989, 1993). Given the purported critical importance of seagrass habitat to the juvenile stages of many commercial fish and invertebrate species, it is not clear why more cases of strong declines in fisheries associated with massive loss of seagrass have not been reported.

In contrast to many species of fish and invertebrates that are found in a range of different nursery habitats, aquatic vegetation (seagrass and algae) alone provides the critical nursery habitat for juvenile tiger prawns *Penaeus esculentus* and *Penaeus semisulcatus* (Haywood et al., 1995; Loneragan et al., 1998; Dichmont et al., 2007; Haywood and Kenyon, 2009). Juvenile brown shrimp *Farfantepenaeus* (formerly *Penaeus*) *aztecus* use aquatic vegetation (saltmarsh) extensively (Minello et al., 1989; King and Sheridan, 2006) but also other shallow structured habitats such as oyster reefs (Stunz et al., 2010). Note that although the subgenera of *Penaeus* where elevated to genera by Pérez-Farfante and Kensley (1997), some controversy surrounds the revised nomenclature and the older names are used for the Australian species following Baldwin et al. (1998) and Lavery et al. (2004). Tiger prawns spawn in deeper and more offshore waters and the planktonic larvae are transported to shallow coastal areas, where as postlarvae, they settle on beds of seagrass and algae, three to four weeks after the eggs are released from the females (Dall et al., 1990; Haywood et al., 1995; Liu and Loneragan, 1997; Haywood and Kenyon, 2009). In Western Australia, significant fisheries for *P. esculentus* are found in the embayments of Exmouth Gulf (21° 50′ S to 22° 30′ S, Fig. 1) and Shark Bay (23° 34′ S to 26° 30′ S), where seagrass beds are found in the shallow inshore areas.

In recent years, the brown tiger prawn, *Penaeus esculentus*, has comprised about 40% of the total annual prawn landings (ca. 1000 tonnes) from the Exmouth Gulf prawn trawl fishery (Caputi et al., 1998; Kangas et al., 2008; Kangas and Sporer, 2010). This species completes its life-cycle within Exmouth Gulf and forms a separate population from that in Shark Bay, about 500 km south of Exmouth. The major environmental feature of the Exmouth region is the semi-arid climate, with an average annual rainfall of about 230 mm. Typically, rainfall in the summer and autumn months (December to May) is associated with the activity of cyclones. In March 1999, Cyclone Vance travelled down the centre of Exmouth Gulf before crossing the coast at the southern end of the Gulf (Fig. 2). The 'eye' of the cyclone straddled Exmouth Gulf and travelled the length of the gulf, with average maximum wind speeds of $>$200 km h^{-1} near the eye, and gusts of $>$279 km h^{-1}, causing extensive damage to the mangroves and seagrasses in inshore areas of the Gulf (Loneragan et al., 2003, 2004; Paling et al., 2008).

In this study, we determined the changes in the distribution, abundance, and species composition of seagrass and macroalgae following Cyclone Vance and investigated how these changes are related to the recruitment to the fishery and the landings of tiger prawns in the Exmouth Gulf fishery. The patterns in the fishery are compared with those in Shark Bay, about 500 km south of Exmouth Gulf, where the inshore habitats were not affected by cyclonic activity at this time. Previous cyclones in the Exmouth region have been associated with both positive and negative effects on tiger prawn landings in Exmouth Gulf, depending on the time of year when the cyclone occurred and its magnitude (Penn and Caputi, 1986; Caputi et al., 1998). However, no information was available on changes in the inshore habitats of Exmouth Gulf following these earlier cyclones. This study therefore provides the opportunity to examine the link between loss of coastal habitat and fisheries production at broad geographic scales for a species with a critical dependency on macrophyte nursery habitats.

2. Material and methods

2.1. The environment

Exmouth and Shark Bay are semi-enclosed embayments in semi-arid, sub-tropical Western Australia (Fig. 1). Exmouth Gulf is a marine embayment open to the north, covering an area of approximately 2200 km^2, with a width of about 40 km and length of 80 km (Fig. 1). The water depth outside the shallow intertidal waters ranges from about 5 m in the south-eastern Gulf to about 20 m in the northern and western regions of the Gulf. Extensive muddy salt flats, up to 10 km wide, border the southern and eastern shores of the Gulf and are intersected by numerous tidal channels (McCook et al., 1995; Brunskill et al., 2001). The intertidal mudflats are lined with dense stands of mangroves, mainly *Avicennia* and *Rhizophora* species, that make up one of the largest mangrove areas in Western Australia (Paling et al., 2008).

Shark Bay, located about 500 km south of Exmouth and 850 km north of Perth comprises two large shallow "gulfs", separated by a peninsula. It is relatively shallow throughout and consists of shallow sand flats, embayment plains, and deeper channels (Nahas et al., 2003). Although 12 species of seagrass have been recorded, the seagrass meadows in the shallower waters are dominated by *Amphibolus antarctica* (Walker et al., 1988; Tyne et al., 2012).

Prior to this study, the only known information on seagrasses and macroalgae in Exmouth Gulf came from a survey in September 1994, which found four species of seagrass (*Cymodocea serrulata, Syringodium isoetifolium, Halophila ovalis* and *Halodule uninervis*) at sites along the eastern shores of the Gulf (McCook et al., 1995). The

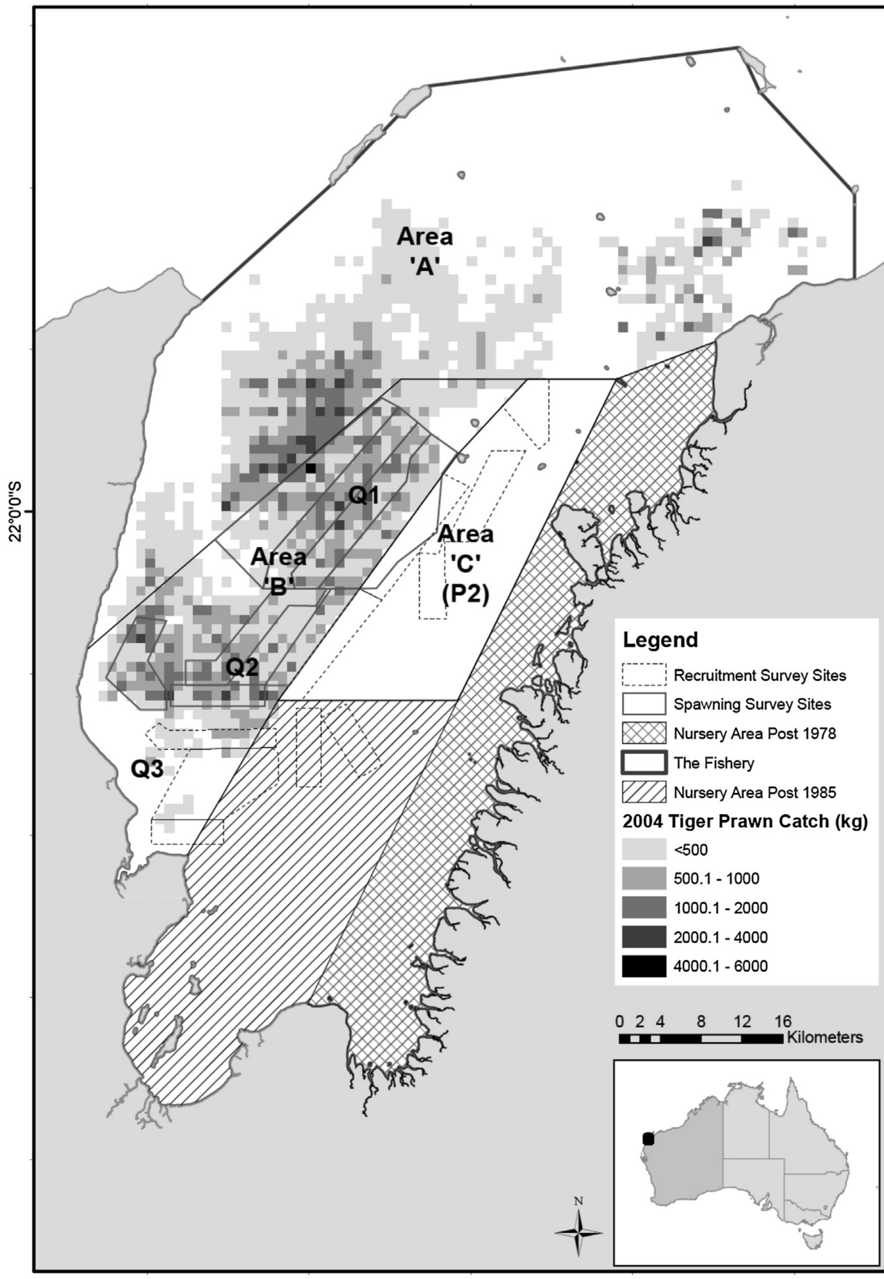

Fig. 1. Location of Exmouth Gulf, Western Australia and prawn survey areas for recruitment (Q3, Q2 and P2) and spawning stock surveys (Q2 and Q1). Main areas in the fishery; areas A (king prawns) and B and C (tiger prawns), nursery area closures (original and extended) and overall catches of tiger prawns in 2004, are also shown.

percentage cover of seagrass was about 5% at most sites, with a maximum cover of 20% (McCook et al., 1995).

Data on the paths of cyclones in the Exmouth region and rainfall at Learmonth were obtained from the Bureau of Meteorology.

2.2. Exmouth Gulf and Shark Bay prawn trawl fisheries

The Exmouth Gulf prawn trawl fishery started in 1963 with 12 boats. This early stage of the fishery was a daylight fishery for banana prawns (*Penaeus merguiensis*) but it changed to mainly a night-time fishery, with no restrictions on the hours to fish or seasonal closures. As the fishery expanded, tiger prawns became the target species and were approximately 60% of the total catch until 1980, with king (*Penaeus latisculatus*) and endeavour prawns (*Metapenaeus endeavouri*) each comprising about 20% of the total landings. Catches of tiger prawns and fishing effort increased rapidly in the mid 1970s before catches declined sharply in the early 1980s due to increases in fishing effort and efficiency that resulted in overfishing (Penn and Caputi, 1986; Caputi et al., 1998).

In 1978, closed areas were implemented on the eastern side of the Gulf, inshore of the fishery, to protect small prawns and their nursery and settlement habitats and these closed areas were expanded in 1986 (Fig. 1). Strict management measures were implemented to control fishing effort on the tiger prawn stocks, including; night time-only fishing (18:00 to 08:00 h), a seasonal closure (November to March), introduction of maximum net headrope size and board size, and the establishment of fishing areas to allow opening and closure of areas (Areas B and C) during the year, and setting threshold catch levels to halt fishing and ensure a constant escapement of prawns to the spawning stock

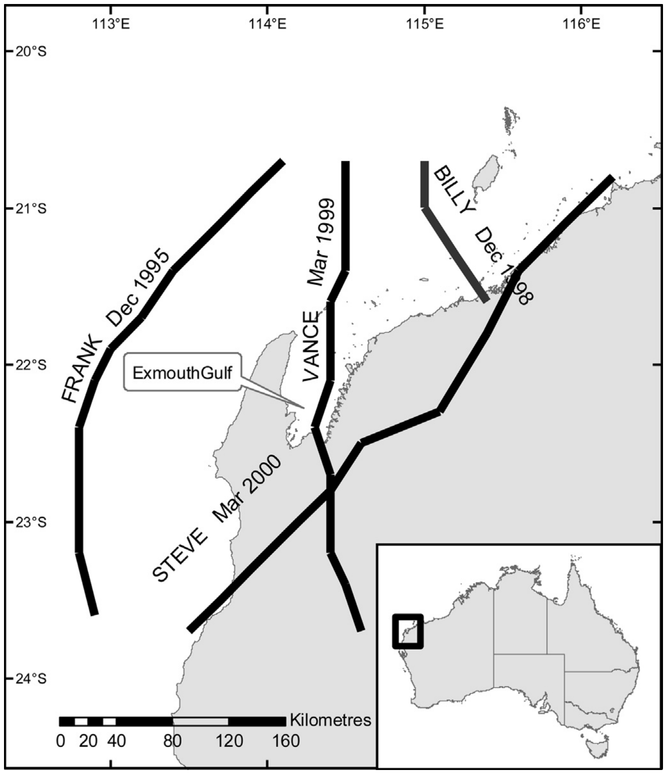

Fig. 2. Paths of Cyclones in the Exmouth Gulf region from 1995 to 2005. Cyclone paths provided by the Bureau of Meteorology. In general, cyclones move from north to south in this region.

each year (Fig. 1). Exmouth Gulf was divided into three regions: Areas A (primarily a king prawns) B (tiger prawn spawning area) and C (tiger prawn recruitment grounds) (Fig. 1). Tiger prawns are fished in waters between 8 and 18 m deep, mainly to the west and southwest in the central part of the Gulf (Area B, Fig. 1), offshore from the beds of seagrass and macroalgae in shallower water. Fishery-independent monitoring of recruitment to the fishery and spawning stock was introduced in the mid-1980s (Penn and Caputi, 1986; Penn et al., 1997; Caputi et al., 1998).

The Shark Bay fishery has had a similar history of development and management to the Exmouth Gulf fishery, including a major decline in tiger prawn stocks in the early 1980s. However, as king prawns were the main target species in Shark Bay, management measures designed to recover tiger prawns were not introduced immediately and tiger prawn stocks did not recover for 10 years (Penn et al., 1995).

2.3. Indices of recruitment, spawning stock and tiger prawn landings

In Exmouth Gulf, fishery-independent surveys of both recruitment and spawning stock were completed using commercial fishing boats from the Exmouth Gulf prawn fishery fitted with conventional otter prawn trawl nets (50 mm cod end mesh size). The trawl nets changed from twin to quad otter trawls in 2000 and the two net types have been calibrated. Since 1985, three recruitment surveys have been completed annually: in early and late March and early April in areas Q3 and P2 and part of the nursery area (Fig. 1) to determine an index of recruitment to the fishery (mean catch rate kg h^{-1}). A total of 10 sites were trawled during the night in each survey, with trawl durations of between 30 and 120 min. Sites were trawled near the quarter moon phase (i.e. the first and last quarters). It was not possible to complete a recruitment survey in mid-March 1999 because of the extreme weather conditions during Cyclone Vance. Spawning stock surveys were carried out during the night at eight sites in August, September and October each year around the last quarter moon phase, in areas Q1 (since 1982) and Q2 (since 1989) (Fig. 1). Over four nights, the sites in Q1 and Q2 are sampled twice on alternate nights, with each trawl lasting 2.5 h.

The mean spawning stock and recruitment indices were calculated for each survey and averaged for each year to calculate annual indices for the whole of Exmouth Gulf. Data on commercial landings, nominal fishing effort (hours trawled, adjusted for changes in headrope length) and catch per unit effort were obtained from fishers' logbooks for Exmouth Gulf and Shark Bay that are completed after each trawl.

2.4. Extent of seagrass in Exmouth Gulf

Qualitative and quantitative surveys of benthic habitats were carried out in 1999, 2000 and 2001 to identify the location of seagrass beds, the critical tiger prawn nursery habitats in Exmouth Gulf (for full details of sampling methods see Kenyon et al., 2003; Loneragan et al., 2004). Further seagrass surveys were carried out by the Western Australian Department of Fisheries in March of 2003, 2005 and 2006 (Fig. 3).

The initial, gulf-wide survey of benthic habitats in June 1999, three months after Cyclone Vance, was used to identify the broad areas where seagrass and algae were located in Exmouth Gulf in water depths of <5 m. Subsequent surveys focussed on the eastern side of Exmouth Gulf, from the central region to the southern shore (Fig. 3). In the initial survey and that of November 1999, qualitative estimates of habitat cover were made by diving along a 30 m transect and recording a visual estimate of the percentage cover of different benthic habitats within 1 m on either side of the transect. In the November 1999 and subsequent surveys, sites were re-allocated to the 0–2.5 m depth zone as there was little evidence of vegetated substrates at depths >2.5 m. From October 1999, quantitative samples were taken of the substratum at randomly selected points in those areas identified as likely to contain seagrass from the June survey and the previous study by McCook et al. (1995). Samples of the substratum and vegetation were taken using a "standard" shovel (area $= 0.07$ m^2), together with a sediment sample (following Poiner et al., 1987). Qualitative estimates of the percentage cover of seagrass and macroalgae were made at the same time as the quantitative sample was taken. Samples of vegetation were taken to the laboratory, sorted to species and the shoot density and above-ground-biomass (wet and dry weight) were determined for each species. The means ($\pm$1SE) for the percentage cover of seagrass, macroalgae and total cover of macrophytes, biomass of macroalgae, and below-ground-biomass, above-ground-biomass and surface area of seagrass, were calculated for each survey in each region. These mean values were then used to calculate a mean for the region in 1999 and 2000. A total of 120 and 137 qualitative samples were taken at different sites in June and November 1999, respectively (Fig. 3). Quantitative samples were taken at 97 and 131 sites between October and December 1999, 341 sites in October and December 2000 (Fig. 3) and 75 sites in December 2001.

The extents of seagrasses and macroalgae were also monitored at five main areas in Exmouth Gulf (a subset of those areas sampled between 1999 and 2001) in March 2003, 2005 and 2006 using a combination of transects, quadrats and recording by video. Qualitative samples were taken at each site by randomly placing four 1 m^2 quadrats on the bottom, and estimating the % cover and species composition in each square at Tent Island, Simpson

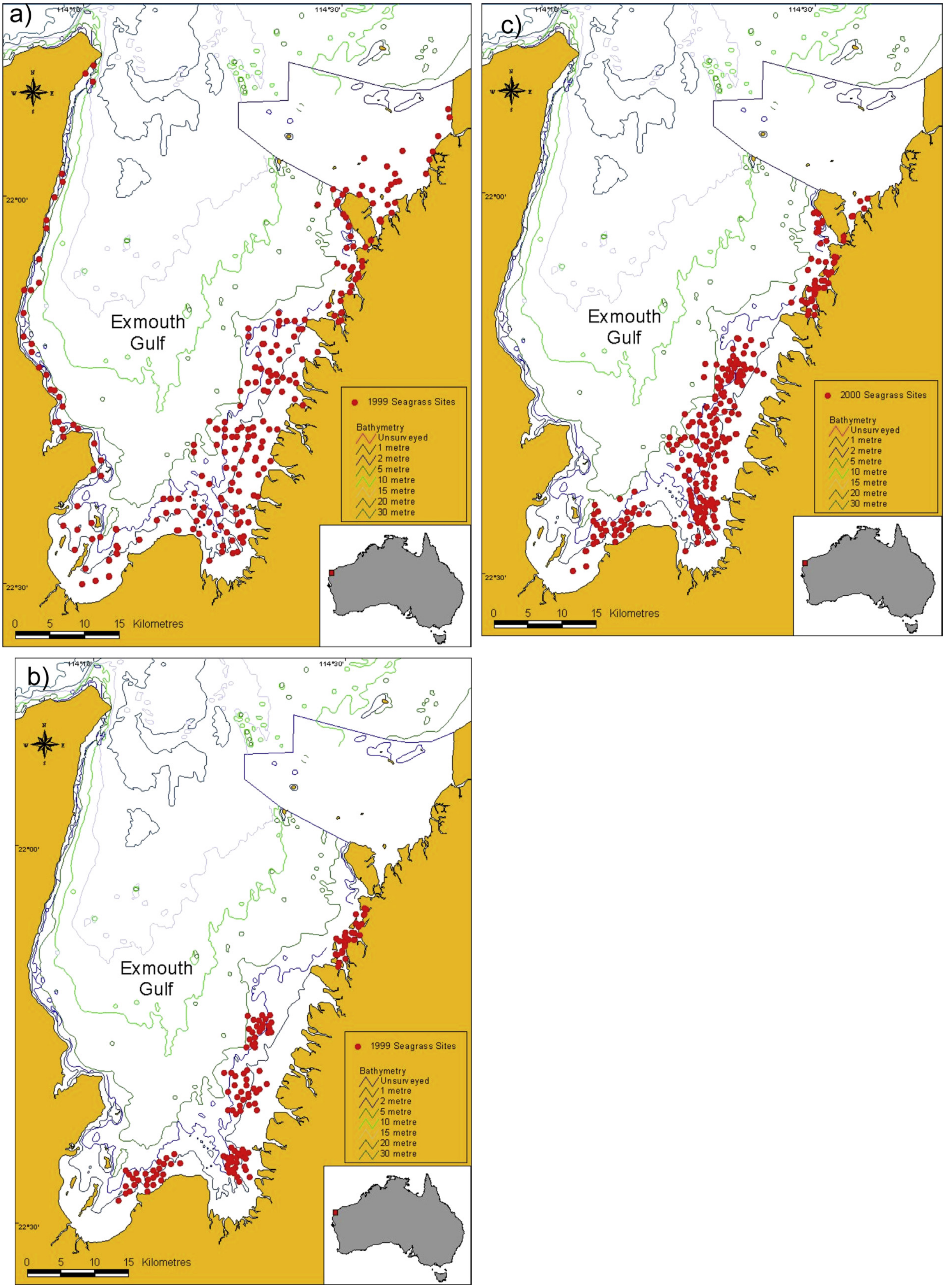

Fig. 3. Seagrass and macroalgal sampling sites in Exmouth Gulf in a) June 1999, b) December 1999 and c) December 2000.

Island, Whalebone Island North, Whalebone Island South and the Sandalwood Peninsula/Gales Bay (Fig. 3); between 11 and 16 sites were sampled in each area. In 2006, Gales Bay was not sampled. The average percentage covers of seagrass and algae were calculated for each region and for the whole of the south-east and eastern part of Exmouth Gulf.

2.5. Macrophyte – prawn relationships

Pearson's correlation coefficients were calculated between the extent (percent cover) of seagrass, macroalgae and total macrophytes i.e. seagrass and macroalgae, and the average annual prawn recruitment index and landings for Exmouth Gulf. Data on the extent of macrophytes were arcsin (√) transformed before analysis. Data on the extent of macrophytes were only available for six years (1999, 2000, 2001, 2003, 2005 and 2006). The relationships between the recruitment index and landings and extent of macrophytes (seagrass, macroalgae and total macrophyte cover) were also explored using multiple regression analyses. For the years before 2002, when macrophyte cover was surveyed in the months from October to December, the cover was related to the recruitment and landings data for the following year, while for years after 2002 when macrophytes were surveyed in March/April, the cover was related to the recruitment and landings data for the same year.

3. Results

3.1. Rainfall and cyclones

Cyclone Vance has been the only major cyclone in the last 40 years to pass through the centre of Exmouth Gulf, travelling from north to south and running parallel to the western and eastern coastlines of the Gulf, before crossing the coast in the south (Fig. 2). The rainfall associated with Cyclone Vance was the second highest rainfall recorded in the months of January to March since 1970, with about 400 mm of rain falling in February and March of 1999. In 2000, 300 mm of rainfall was recorded in March, associated with Cyclone Steve, which crossed the coast north of Exmouth Gulf and travelled inland before returning to sea (Bureau of Meterology data). A total of 33 cyclones were recorded between 1970 and 2009. The frequency of cyclones was highest in the months of February (11) and March (11), followed by January (7), with only four cyclones were recorded in December (3) or April (1). Only two cyclones were recorded within 200 km of Carnarvon, Shark Bay between 1970 and 2009 (Bureau of Meterology data).

3.2. Extent of seagrass and macroalgae in shallow, near shore areas

In June 1999, three months after Cyclone Vance, the mean percent cover of seagrass in all regions was very low (mean cover $< 0.5\%$) and seagrass was found at less than one third of the sites (Table 1a). The proportion of sites where macroalgae (mostly drift algae) was found (40%) was slightly greater than that of seagrass. The areas where seagrass were most commonly found included the southern and south-eastern parts of the Gulf (Sandalwood/Gales and to the north and south of Whalebone Island, Table 1, Fig. 4a). By November and December 1999, the proportion of sites with seagrass and the mean % cover of seagrass had increased (Table 1). By October and November 2000, about 18 months after Vance, 65 and 59% of all sites had seagrass and macroalgae, respectively. Although the overall mean percentage cover of seagrass remained relatively low ($<10\%$), in eight locations (south of Whalebone Island), its presence had increased to greater than 80% of sites (Fig. 4b). The percentage cover of seagrass increased greatly in 2001 and exceeded 30% in each of the three regions that were sampled (Table 1).

From 2003 until 2006, seagrass and macroalgae were present at most sites in the south-west and south-eastern areas of the Gulf (Table 1a). Macroalgae was present at virtually all sites in the northeast, and seagrass was found at 50–94% of the sites (Table 1a). The mean percent cover of seagrass continued to increase in all areas sampled from 2000 to a peak of $\sim 50\%$ in 2001 and 2003. The cover of seagrass decreased markedly to about 5% in 2005 and 2006 (Table 1b). During this time, the presence of *Halophila spinulosa*

Table 1
The a) percentage of sites with macrophytes (seagrass or macroalgae) and seagrass alone (in parentheses), and mean percent cover of b) seagrass and c) macroalgae in 5 regions of Exmouth Gulf from 1999 until 2006. n.s. = not surveyed.

Year	Region					Overall
	Sandalwood/Gales	Whalebone Is. S	Whalebone Is. N	Simpson Is	Tent Is.	
a) Percentage of sites with macrophytes (seagrass only)						
Jun 1999	62 (46)	38 (31)	41 (37)	50 (0)	19 (13)	40 (29)
Nov1999	38 (69)	65 (69)	60 (50)	23 (31)	57 (0)	52 (44)
2000	45 (74)	80 (84)	54 (72)	47 (21)	37 (16)	59 (65)
2001	75 (95)	69 (98)	29 (95)	n.s.	n.s.	58 (96)
2003	77 (92)	94 (75)	88 (94)	64 (64)	92 (62)	84 (78)
2005	67 (75)	79 (64)	88 (82)	90 (50)	92 (62)	83 (64)
2006	n.s.	81 (56)	88 (94)	64 (55)	92 (77)	82 (72)
b) Mean percent cover of seagrass						
Jun 1999	0.31 ± 0.11	0.25 ± 0.10	0.11 ± 0.05	0	0.16 ± 0.13	0.17 ± 0.04
Nov 1999	1.07 ± 0.38	3.43 ± 1.18	1.7 ± 0.8	0.17 ± 0.10	0	1.45 ± 0.38
2000	3.17 ± 0.75	18.1 ± 2.58	3.81 ± 0.88	0.06 ± 0.03	0.16 ± 0.11	7.84 ± 1.02
2001	30.2 ± 4.1	45.5 ± 4.1	61.2 ± 4.5	n.s.	n.s.	45.4 ± 2.7
2003	48.2 ± 9.4	41.1 ± 9.0	73.0 ± 7.9	46.7 ± 14.1	31.3 ± 10.5	48.9 ± 4.7
2005	2.7 ± 0.9	0.9 ± 0.3	2.7 ± 0.7	3.8 ± 1.6	14.5 ± 7.2	5.0 ± 1.5
2006	n.s.	1.0 ± 0.5	2.8 ± 0.7	4.0 ± 2.2	16.4 ± 9.3	5.4 ± 2.2
c) Mean percent cover of macroalgae						
Jun 1999	1.2 ± 0.75	1.04 ± 0.93	0.98 ± 0.75	25.01 ± 17.1	0.44 ± 0.33	2.77 ± 1.45
Nov 1999	3.16 ± 1.91	3.72 ± 1.71	1.16 ± 0.77	6.92 ± 3.65	5.68 ± 2.41	3.99 ± 0.94
2000	0.94 ± 0.24	3.94 ± 0.56	4.62 ± 1.53	2.48 ± 1.71	2.79 ± 1.28	3.25 ± 0.51
2001	3.23 ± 0.61	4.71 ± 0.81	4.89 ± 2.37	n.s.	n.s.	4.28 ± 0.82
2003	6.8 ± 1.6	26.2 ± 8.1	13.9 ± 6.1	25.7 ± 12.5	37.0 ± 10.3	21.6 ± 3.8
2005	0.9 ± 0.3	7.4 ± 6.0	10.6 ± 4.6	12.7 ± 6.3	26.1 ± 9.3	11.6 ± 2.8
2006	n.s.	7.2 ± 2.1	11.3 ± 5.1	24.6 ± 12.1	18.5 ± 7.8	14.3 ± 3.4

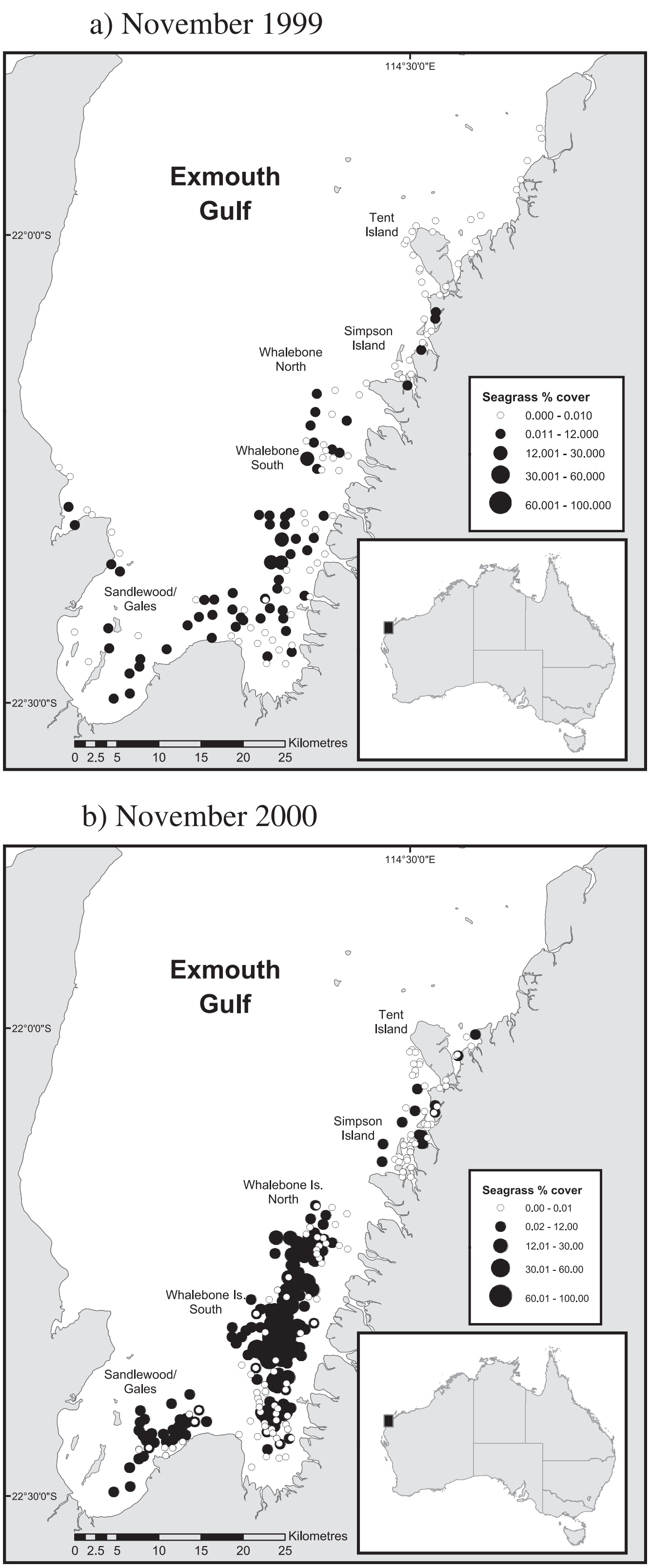

Fig. 4. Percentage cover of seagrass at sites in Exmouth Gulf, Western Australia, in November of a) 1999 and b) 2000, seven and 19 months after Cyclone Vance, respectively.

declined from 53.6% of sites 2003 to less than 2% of sites in 2005 and 2006, while that of *Syringodium isoetifolium* declined from 42% to ≈20%. The mean percent cover of macroalgae was <5% from 1999 until 2001 but was higher than 11% from 2003 until 2006, with a maximum cover of 21.6% in 2003 (Table 1c). The total mean cover of macrophytes increased from 1999 (4.2%) to 2003 (70.5%) and declined greatly in 2005 and 2006 (16.6 and 19.7%, respectively).

Only two species of seagrass, *Halodule uninervis* and *Halophila ovalis*, were recorded from the 60 sites sampled in November 1999 and each was represented in 20–30% of the samples (Table 2). The number of species of seagrass recorded increased from two (*H. uninervis* and *H. ovalis*) in November to four in December 1999 and six by November 2000. Three species were found at over 35% of the sites in December 2001 (Table 2). The larger, longer-leaved species (*Cymodocea serrulata* and *Syringodium isoetifolium*) were first recorded in October–November 2000. A number of macroalgal species were found in Exmouth Gulf, mainly in the genera *Sargassum, Caulerpa, Udotea, Padina* and *Halimeda*. Some of the brown algae, particularly *Sargassum* spp., provided a vertical canopy height of between 200 and 500 mm, particularly in the Simpson and Tent Island areas.

The means for the below- and above-ground biomass and surface area of seagrass per m^2 of substratum were very low in in all five regions in October to December 1999 (Fig. 5). In 2000, they were much higher in Gales Bay and Whalebone North and South than in 1999 but changed very little at Simpson and Tent Island (Fig. 5).

3.3. Recruitment, spawning stock and landings of prawns

The mean annual recruitment index for tiger prawns in Exmouth Gulf ranged from 17 to 54 between 1985 and 1994, was relatively stable between 1995 and 1999 (25–35), before declining to 21 in 2000 and 14 in 2001, which was the lowest recorded recruitment between 1985 and 2006 (Fig. 6a). The recruitment index increased to a maximum of 55 in 2003 and declined to 25 in 2006 (Fig. 6a), after a decline in cover of seagrass and macroalgae (Tables 2 and 3). In 1999, the year of Cyclone Vance, the recruitment index was 28.5, slightly below the long-term recruitment index of 31 for the years between 1985 and 2006. The strength of recruitment varied between the two areas e.g. the recruitment index was greater in Q3 than P2 between 1995 and 1999 but was greater in P2 than Q3 between 2003 and 2005 (Fig. 6a).

In general, the mean annual index of spawning stock was less variable between years than the recruitment index (Fig. 6b cf 6a).

Table 2
Percentage of all sites where different species of seagrass were recorded in Exmouth Gulf, Western Australia. - = not recorded. A broad-leaved morph of *Halodule uninervis* was also recorded in October and November 2000 (0.8 and 1.3% of sites) and in December 2001 (2.5% of sites).

Seagrass species	Month and year of survey							
	Nov-99	Dec-99	Oct-00	Nov-00	Dec-01	Mar-03	Mar-05	Mar-06
Cymodocea serrulata	–	–	0.4	4.6	35.8	40.6	54.5	50.9
Halodule uninervis	28.0	35.0	20.6	33.1	70.0	40.6	54.5	38.6
Halophila ovalis	18.7	21.7	14.8	27.8	8.3	10.1	24.2	12.3
Halophila spinulosa	–	1.7	5.3	9.3	68.3	53.6	1.5	1.8
Halophila descipiens	–	1.7	5.8	9.9	0	–	–	–
Syringodium isoetifolium	–	–	–	1.3	14.2	42.0	22.7	17.5
Total number of species	2	4	5	6	5	6	6	6
Total number of sites	60	75	243	151	120	69	66	57

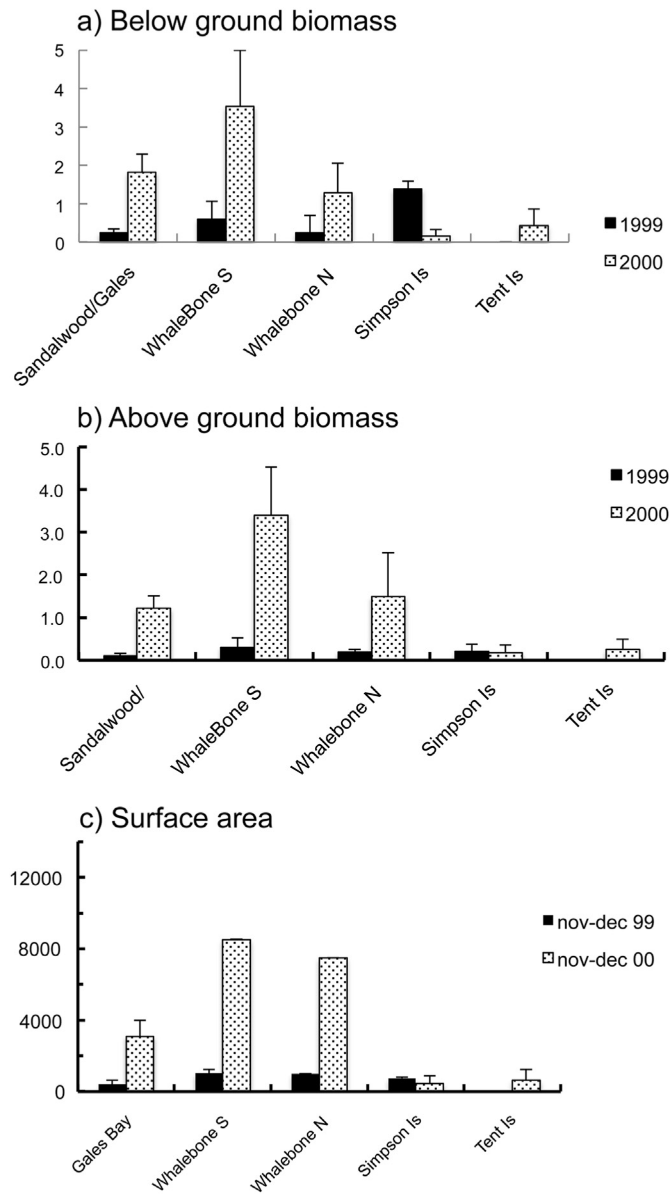

Fig. 5. Mean (±1SE) below- and above-ground biomass, and surface area of seagrass (m^2 per m^2 of substratum) in five regions in Exmouth Gulf in October–December of 1999 and 2000.

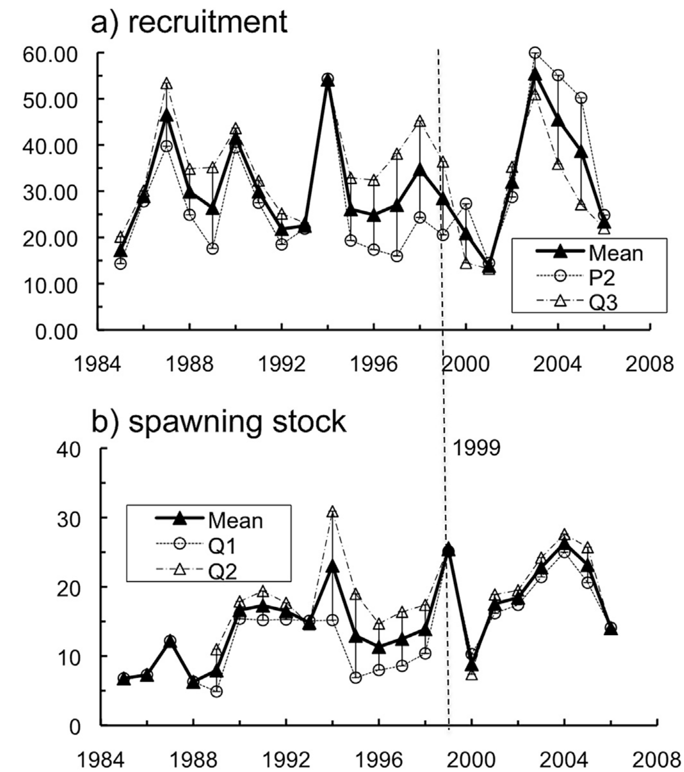

Fig. 6. Annual average indices of a) recruitment and b) spawning stock of tiger prawns (*Penaeus esculentus*) from fishery independent surveys in Exmouth Gulf, Western Australia between 1985 and 2006. Dashed vertical line is 1999, year of Cyclone Vance.

The second highest spawning stock index (25) was recorded in 1999 after Cyclone Vance, and was followed by one of the lowest on record in 2000 (8.9), which is about 60% of the mean long-term index between 1985 and 2006 (15.3) (Fig. 6b). The spawning stock index increased after 2000 to a maximum of 26 in 2004 before declining to 14 in 2006. In general, the average spawning stock index was higher in area Q2 than in Q1 (Fig. 6b).

In Exmouth Gulf, landings of tiger prawns and nominal fishing effort increased rapidly from the start of the fishery in the 1960s, reaching a maximum of 1239 metric tonnes in 1975 before declining greatly to only 77 tonnes in 1983 (Fig. 7). Since the effort reductions in the early 1980s to improve the breeding stock, landings increased and ranged from about 205 to 682 tonnes between 1987 and 1999 (Fig. 7). The landings of tiger prawn landings fell markedly from 450 tonnes in 1999 to 82 tonnes in 2000, the year following Cyclone Vance (Fig. 7). Since 2000, tiger prawn landings increased steadily from about 205 tonnes in 2001 to 630 tonnes in 2003 and 2004 but were lower in 2005 and 2006 (416 and 258 tonnes, Fig. 7).

The adjusted nominal fishing effort exceeded 50 000 h of trawling between 1976 and 1981 but because of management measures, declined to about 35 000 h by the mid 1990s and then to 25 000 h in the mid 2000s (Fig. 7). The CPUE (using adjusted effort) was 27.5 kg h^{-1} in 1975, declining to the lowest on record of 2–3 kg h^{-1} in 1982 and 1983. Since then, the CPUE has been greater than 5 kg h^{-1} in all years, except 2000 (2.5 kg h^{-1}), the initial year of prawn recruitment after the cyclone. No decline in tiger prawn landings or CPUE were recorded in Shark Bay at this time, with landings remaining high in 2000 (689 t, 90 t higher than in 1999) and CPUE ranging only from 9.6 to 13.2 kg h^{-1} between 1997 and 2001 (Fig. 7).

The index of recruitment to the fishery and landings of prawns in Exmouth Gulf were highly correlated between 1985 and 2006 ($r = 0.90$, $n = 22$) and the six years when data were available for prawns and macrophyte habitat ($r = 0.88$, $n = 6$). The correlations between spawning stock and recruitment ($r = 0.53$, $n = 22$) and

Table 3
Pearson correlation coefficients between the percentage cover of seagrass, macroalgae and total macrophytes (all arsin ($\sqrt{p}$) transformed) and the recruitment and landings of tiger prawns in Exmouth Gulf. ($n = 6$). Superscript shows the probability of the correlation (1-tailed test) and bold superscripts show significant correlations at $P < 0.05$.

Variable	Variable			
	Seagrass	Macroalgae	Total macrophytes	Recruitment
Macroalgae	$0.35^{0.50}$			
Total Macrophytes	$0.96^{\mathbf{0.002}}$	$0.59^{0.21}$		
Recruitment	$0.67^{0.07}$	$0.78^{\mathbf{0.04}}$	$0.81^{\mathbf{0.03}}$	
Landings	$0.80^{\mathbf{0.03}}$	$0.75^{\mathbf{0.04}}$	$0.90^{\mathbf{0.007}}$	$0.93^{\mathbf{0.008}}$

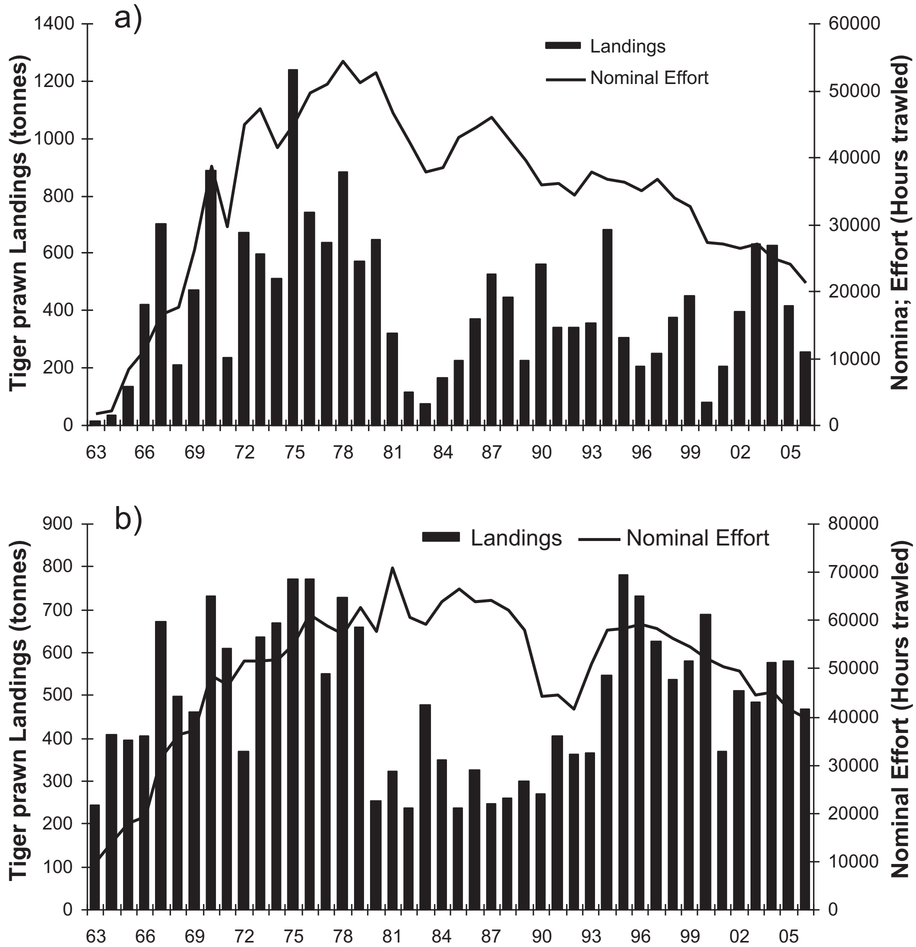

Fig. 7. Annual landings of tiger prawns *Penaeus esculentus* and nominal annual fishing effort (hours of trawling) in the prawn trawl fisheries of a) Exmouth Gulf and b) Shark Bay Western Australia, between 1963 and 2006.

spawning stock and landings ($r = 0.62$, $n = 22$), were weaker than those for recruitment and landings.

The percentage cover of seagrass was not correlated with that of macroalgae ($r = 0.35$, $P = 0.50$) but was correlated significantly with the percentage cover of total macrophytes ($r = 0.96$, $P = 0.002$) (Table 3). The recruitment and landings of tiger prawns were significantly correlated with cover of total macrophytes, and landings were also significantly correlated with the cover of seagrass and macroalgae (Table 3). The mean percent cover of total macrophytes was the only significant variable fitted in the multiple regression equations for the recruitment index and landings of tiger prawns (Fig. 8). The total cover of macrophytes had a better fit than seagrass or macroalgae fitted separately. Rainfall was not correlated significantly with recruitment or landings between 1985 and 2006 ($r = -0.14$ and -0.12, respectively, $n = 22$) or for the six years when data were collected on macrophytes ($r = -0.40$ and -0.31, respectively, $n = 6$).

In most years, small prawns (<30 mm carapace length [CL]) dominated the recruitment surveys. In 1999, 2001, the modal CL for male prawns was about 25 mm, with a small number of males longer than 30 mm CL. In these years, female prawns had a modal size of 27–29 mm CL and about 70% of the prawns were less than 30 mm CL. These typical size distributions contrast with that in 2000, when the modal size of male (30–32 mm CL) and female prawns (38 mm CL), was 5–10 mm longer, indicating that the population consisted mainly of prawns that had been present in late 1999 i.e. they were mainly residual prawns, with few new recruits. In contrast to other years, about 70% of the prawns were 30 mm CL or longer in 2000. These residual prawns remained within the area of the fishery probably due to low fishing effort and conservative harvesting of prawns during 1999.

4. Discussion

4.1. Changes in seagrass, macroalgae and mangroves

Cyclone Vance caused extensive loss of seagrass, macroalgae and mangrove habitats in Exmouth Gulf. The littoral seagrass community identified by McCook et al. (1995) appears to have been removed by the mechanical forces associated with cyclonic winds and waves. Mangroves were also decimated by these cyclonic forces, with an estimated 44% loss of mangrove cover after the Cyclone (Paling et al., 2008). Although no data were available for the extent of seagrass and macroalgae in the years immediately prior to Cyclone Vance (1999), anecdotal evidence from pearl divers in the eastern Gulf and field observations three months after Cyclone Vance, confirm that it caused a very extensive loss of littoral macrophytes and extensive damage to the mangroves along the shores of the Gulf (see also Paling et al., 2008). For example, along the north-western coastline of the Gulf (i.e. in clear water, exposed areas south-east of North West Cape), diving observations during the broad scale habitat surveys in June 1999 showed clear evidence of the mechanical impacts of the cyclone on coral – only a carpet of coral rubble and patches of bare rock could be found.

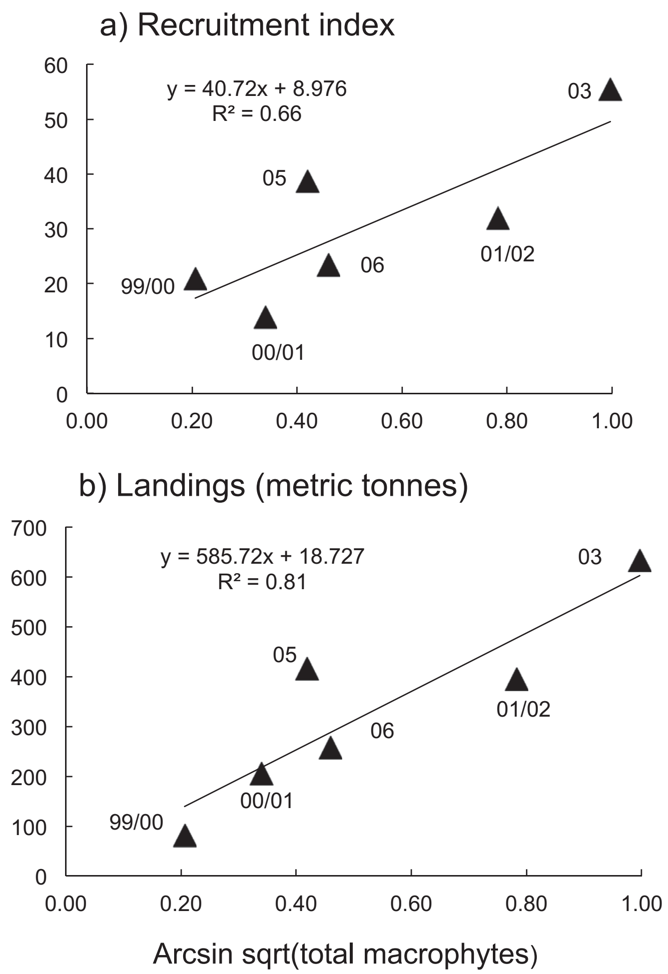

Fig. 8. Relationship between mean percentage cover of total macrophytes (seagrass and macroalgae, arcsin $\sqrt{p}$ transformed and a) the recruitment index and b) landings of tiger prawns *Penaeus esculentus* in Exmouth Gulf, Western Australia.

Among the shallow soft sediment habitats in the Gulf, unconsolidated fine silts were evident and virtually no epibenthos, nor rooted biota, were seen. The loss of seagrass and macroalgae following Cyclone Vance therefore appears to have been immediate and across the whole of Exmouth Gulf. In contrast, no cyclones or evidence of loss of littoral macrophyte habitat were recorded in Shark Bay, 500 km south of Exmouth Gulf, at this time.

4.2. Changes in prawn population

The loss of the seagrass and macroalgal communities greatly reduced the extent of settlement habitat for prawn postlarvae and the juvenile prawn nursery grounds, which was probably the major factor leading to the decline in recruitment to the fishery, spawning stock and landings of tiger prawns in 2000, the year after Cyclone Vance, and in 2001. Cyclone Vance struck in mid-March 1999, after many of the juvenile prawns, spawned in 1998 are likely to have emigrated from their seagrass habitats to deeper, unvegetated habitats in the Gulf (see O'Brien, 1994; Loneragan et al., 1994, 1998). This movement away from the shallows, and the reduction in dependence on seagrass by larger juveniles and sub-adult prawns (Somers, 1987; Loneragan et al., 1994), is likely to have minimised the effects of the cyclone on the prawn population in 1999. The increase in turbulence of the water may, in fact, have enhanced the survival of prawns in more offshore waters by increasing turbidity and reducing predation by visual predators and the cyclonic disturbance of sediments may have stimulated the release of nutrients, leading to an increase in primary production and food supply. This potential positive effect of cyclones has been noted previously when cyclones in late summer, e.g. February 1975, have resulted in good landings (Fig. 7; Penn and Caputi, 1986).

The indices of prawn recruitment to the fishery and spawning stock show that the decline in prawn landings in 2000 was not due to a depleted prawn spawning stock in the previous year. In 1999, the recruitment index and landings were similar to their average values since 1987, while the spawning stock index was close to the highest on record. In late 1999 and early 2000, the extent of macrophyte habitat available for recently spawned postlarval tiger prawns to settle and juveniles to grow, was likely to have been much lower than in the years immediately prior to Cyclone Vance. The loss of macrophyte habitat following the cyclone is likely to have affected the total number of postlarval prawns that settled successfully on the seagrass beds and macroalgae in 2000 and 2001 (see Liu and Loneragan, 1997; Loneragan et al., 1998), and as a consequence, reduced greatly the carrying capacity of Exmouth Gulf for juvenile tiger prawns. In Shark Bay, where the inshore seagrass beds were not disturbed by cyclones, the carrying capacity of the Bay for the tiger prawn fishery is unlikely to have been affected by habitat loss, and the landings of tiger prawns did not decline in 2000 and 2001.

The much lower cover of seagrass and macroalgae is also likely to have led to slower growth and lower juvenile survival in the shallow waters (Kenyon et al., 1995; Loneragan et al., 1998, 2001; Ochwada et al., 2009; Ochwada-Doyle et al., 2010). Laboratory studies of predation have found that the predation rates on tiger prawns by a visual fish predators are about three times higher on bare sand compared with high biomass seagrass (>100 g per 100 m^2) and higher on low (<10 g per 100 m^2) than high biomass seagrass (Kenyon et al., 1995; see also; Laprise and Blaber, 1992). Moreover, behavioural studies have shown that postlarval and very small juvenile brown tiger prawns do not bury – they seek refuge on structured habitats such as seagrass and macroalgae (Kenyon et al., 1995; Liu and Loneragan, 1997; Loneragan et al., 1998). When little structure is present, these small prawns are much more exposed to visual predators (Kenyon et al., 1995).

The peak occurrence and cover of macrophytes was recorded in 2003, when the prawn recruitment index and landings of tiger prawns were the highest following Cyclone Vance. The cover of macrophytes, particularly seagrass, declined markedly in 2005 and 2006 and the prawn recruitment index and landings also declined, but not to the same extent as those recorded in 2000. The decline in seagrass was mainly due to a reduction in the cover of *Halophila spinulosa* and secondarily *Syrogodium isoetifolium*. Since no major cyclonic disturbances were recorded in the system at this time, this decline of these seagrass species appears to be related to their natural variability in Exmouth Gulf.

Seagrasses are very responsive to change in the light environment and pulses of turbidity can lead to a rapid decline in seagrass biomass and shoot density (e.g. Longstaff and Dennison, 1999). Large variations in the biomass and presence/absence of *Halophila* spp and *Halodule uninervis* have been reported elsewhere in Australia. For example, at Abbot Point central Queensland, the presence of *Halophila spinulosa*, *Halophila ovalis* and *Halodule uninervis* in seagrass meadows varied seasonally and initially, *H. spinulosa* showed strong recovery from a seed bank in experimentally cleared plots (Unsworth et al., 2010). *Halophila* species, including *H. spinulosa* in the deeper waters, were the first to recover after flood and cyclone related loss of seagrass in Hervey Bay, Queensland Australia (Preen et al., 1995). In stable sub-tropical seagrass communities, *H. spinulosa* is usually found at the lower depth extremity of the seagrass bed where light levels are at the lower limits to support growth; or in deep water, ephemeral banks (Preen et al., 1995; Abal and Dennison, 1996).

This is one of the few studies to show strong evidence of a decline in the extent of coastal habitats linked to a decline in fishery production, probably because of the strength of the dependency of the postlarval and juvenile prawns on aquatic macrophytes and the almost total loss of seagrass from the whole of Exmouth Gulf. Few other species of fish or invertebrates have such strong dependencies on aquatic macrophytes and few other studies have witnessed such devastation in such a short time period e.g. the 70% loss of seagrass in Westernport Bay, south-eastern Australia, took place over two decades (Jenkins et al., 1993; Hobday et al., 1999; Gillanders, 2006), the 60% loss of seagrass in Cockburn Sound, Western Australia took place over 25 years (Vanderklift and Jacoby, 2003) and the 80% loss of seagrass in Galveston Bay, Texas, was recorded over 30 years (Stunz and Minello, 2001). In this latter system, despite the massive decline in seagrass, new settlers of red drum (*Sciaenops ocellatus*) continued to be found and may have been using alternative habitats such as salt marsh, oyster reef, or non-vegetated habitats (Stunz et al., 2010). In many systems, the reduction in aquatic vegetation has been gradual, resulting in fragmentation of seagrass patches, which can lead to an increase in linear extent of habitat and increased production and diversity (Boström et al., 2006; Connolly and Hindell, 2006; Bell et al., 2008), until the linear extent of habitat also declines.

4.2.1. *Recovery of the tiger prawn fishery and seagrasses*

During the history of the Exmouth Gulf fishery, the landings of tiger prawns have shown both positive and negative impacts following cyclones, depending on the timing and strength of the cyclone (Caputi et al., 1998). Unfortunately, data on the extent of seagrass and macroalgae were available only for a limited number of years following Cyclone Vance and not during the time of any other cyclones in the region. In 1971, very low landings were recorded following a late January cyclone but the landings in 1970 and 1972 were high, which suggests that this cyclone may have had an immediate impact on the survival of juveniles in the seagrass beds without having a major impact on the seagrass beds. The winds during the 1971 Cyclone (Beverley) ($\sim$100 km h^{-1}) were, however, much less severe than those during Cyclone Vance, and the substratum would have been much less disturbed. The high landings in the year following Cyclone Beverley suggest that the inshore habitats were not affected by this event. In 1975, a cyclone in February (Rita, maximum wind speeds of $\sim$100 knots km h^{-1}) was followed by record landings in 1975 and 1976, which suggests that prawn catches may have been enhanced through a higher turbidity and increased food in the more offshore waters (see Caputi et al., 1998).

The tiger prawn stocks in Exmouth Gulf have shown great resilience to recover from low levels of stock due to overfishing (77 t in 1983) and Cyclone Vance (80 t in 2000). The recovery in 1983 was facilitated by management restrictions to ensure the maintenance of the breeding stock by limiting fishing – it took about four years for the fishery to recover from this low in 1983. The low levels of tiger prawn stocks after Cyclone Vance showed a similar recovery time after a major natural perturbation to the benthic habitat. Tiger prawn catches declined in 2000, due to low stock levels and restricted fishing on this species. Indices for recruitment and spawning stock were also low in 2000. Seagrass and macroalgal cover recovered slightly in 2000 but covered a much greater area in 2001 and the total macrophyte cover had increased greatly by 2003. This was matched by an improvement in the prawn recruitment index in 2002 and a record recruitment in 2003. This fast recovery of seagrass in Exmouth Gulf is similar to the three-year time for seagrass to recover from the disposal of dredge spoil in the Laguna Madre, Texas (Sheridan, 2004) and the time taken for seagrass and their associated epifaunal fish and invertebrate assemblages to establish after the subsidence of salt marsh in Galveston Bay, Texas (King and Sheridan, 2006). The mangroves of Exmouth Gulf had also recovered 68% of their area four years after Cyclone Vance (Paling et al., 2008).

These fast recovery rates of seagrass contrast with that recorded in the Gulf of Carpentaria in tropical Australia, where seagrasses took 10-years to recover following a major cyclone (Poiner et al., 1989, 1993). It also contrasts with the recovery time for seagrass in sub-tropical Hervey Bay, eastern Australia, where about 1000 km^2 of seagrass was destroyed by a cyclone and flooding. Two years after this event, seagrasses in shallow water showed little sign of recovery, while some seagrass (predominantly *Halophila decipiens*) returned to deeper sites (>10 m) (Preen et al., 1995).

The ability of seagrass beds to recover following storm damage appears to be related to the presence of a suitable seed bank in the sediments (Boström et al., 2006; Hammerstrom et al., 2006; Bell et al., 2008), species-specific characteristics that determine seagrass's resilience to burial and uprooting (Cabaço et al., 2008), and the degree to which the sediment is disturbed, i.e. whether there was significant sediment deposition or whether sediment was scoured from the seagrass bed (Fourqurean and Rutten, 2004). Following Cyclone Vance, virtually all the above-ground components of the seagrass in Exmouth Gulf were obliterated, however some root stock was found within a few centimetres of the sediment surface. The fast recovery of the seagrasses suggests that there was an adequate seed bank within the sediment and that the deeper sediments were not disturbed to a major degree. The disruption of the sediments in the seagrass beds and intertidal mangrove areas with associated freshwater inflow following heavy rainfall may have also provided a stimulus to primary production following Cyclone Vance.

In addition to the impacts of Cyclone Vance on the recruitment and landings in the fishery, the loss of macrophytes, particularly seagrass, appears to have caused dugongs, *Dugong dugong*, to leave Exmouth Gulf and move south to Shark Bay (Gales et al., 2004). This species feeds on seagrass and the estimated numbers of dugong in Exmouth Gulf declined from about 1000 in the five years prior to Cyclone Vance to 200, three months after the Cyclone. The estimated population in Shark Bay, 500 km south of Exmouth Gulf, increased from 10 000 to 14 000 individuals at the same time, apparently partly due to the movement of individuals from Exmouth Gulf. This movement appears to have been driven by disturbance and loss of dugong foraging habitat.

The loss of a seagrass and macroalgae in Exmouth Gulf and the consequent decline of fishery landings have a clear message for the management of coastal natural resources. The maintenance of seagrass and macroalgal communities in coastal embayments and shallow-water environments is critical for the long-term sustainability of some fisheries resources. The significant of the loss of these habitats to coastal ecosystems, and the services they provide, has been highlighted in a meta-analysis by Waycroft et al. (2009). The cyclonic impacts on natural habitats, and subsequent reduction in the harvest of tiger prawns from Exmouth Gulf, indicate that anthropogenic processes which impact fishery nursery habitats close to urban or agricultural areas may have flow-on effects for local food availability. If, as predicted by some climate change scenarios, the frequency and severity of cyclones increases in north-western Australia, the ecosystem of Exmouth Gulf is likely to be disturbed more frequently, leading to greater variability in coastal habitats, and as a consequence, prawn recruitment and landings. Fishery management will need to continue be responsive to episodic declines in prawn stocks as a result of changes in the nursery habitats, to ensure that the breeding stock is protected and the fishery is sustainable.

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